Graft Compatibility of *Citrus* with Plants in the *Aurantioideae* and Their Susceptibility to Citrus Tristeza Virus

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ABSTRACT

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Wild relatives of citrus, including 22 species in 19 genera, were evaluated for susceptibility to citrus tristeza virus (CTV). They were grafted onto rootstocks of *Citrus* spp., graft-inoculated with a severe strain of CTV, with the exception of a seedling of Sydney hybrid (a hybrid between species of *Microcitrus*), which was graft-inoculated to its stem directly. All the species used were graftable to *Citrus*; however, the rate of graft success varied from 27 to 100%, and growth varied markedly. *Severinia buxifolia, Atalantia monophylla, A. citroides, Fortunella polyandra, Clymenia polyandra, Swinglea glutinosa, Feronia limonia,* and *Feroniella lucida* grew as well as *Citrus* grafted onto *Citrus*. Other species grew poorly or very poorly. *Fortunella polyandra, Clymenia polyandra, Microcitrus australis*, Sydney hybrid, *Eremocitrus glauca, Atalantia monophylla*, A. *citroides, Citropsis articulate, Pleiospermium* sp., *Hesperethusa crenulata, Swinglea glutinosa, Aeglopsis chevalieri, Clausena excavata, C. lansium,* and *Merrillia caloxylon* were infected with CTV based on double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) using polyclonal antibodies against CTV. On the other hand, no evidence of CTV infection was found in *Severinia buxifolia* brachytic form, *Triphasia trifolia, Aegle marmelos, Feronia limonia, Feroniella lucida, Glycosmis pentaphylla, Murraya koenigii,* and *M. paniculata*. Two sources of *Severinia buxifolia* from different stocks showed different responses to CTV.

Wild relatives of citrus may have desirable traits, such as resistance to pests and pathogens when used as rootstocks, or they may serve as sources of germ plasm for genetic improvement of citrus (14,15). However, *Citrus* cannot be crossbred with its wild relatives, except with some that are closely related (9). Recent progress in protoplast fusion and formation of somatic hybrids has made it possible to bypass sexual incompatibility. A number of somatic hybrids among *Citrus* and its related genera have been reported (6,7,13,16).

To use citrus relatives for breeding, we must know their useful traits, and these are not well understood. Bitters et al. (1,2) reported the performance of some citrus relatives as rootstocks for *Citrus*. Knorr (11), and Müller and Garnsey (12) investigated the CTV susceptibility of species within the orange subfamily *Aurantioideae.*

Trifoliate orange *(Poncirus trifoliata* (L.) Raf.), closely related to *Citrus*, is generally immune to CTV, but some genotypes are susceptible (18,21). The inheritance of immunity in hybrids of trifoliate orange has been demonstrated (18,19).

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The purpose of this study was to evaluate wild relatives of citrus for susceptibility to CTV, and many immune species that were graft-compatible with rootstocks of *Citrus* were identified.

MATERIALS AND METHODS

Plant materials. The classification of plants in the *Aurantioideae* was according to the system by Swingle and Reece (14). Twenty-three species from 19 genera in the *Aurantioideae* and Sydney hybrid, which is a hybrid between *Microcitrus australis* (Planch.) Swing. and *M. australasica* (F. Muell.) Swing., were examined (Table 1). Two different sources and one form (brachytic form) of *Severinia buxifolia* (Poir.) Tenore were used.

Grafting. Scions of each species originated from a single tree. The scions, except for Sydney hybrid, were grafted onto seedlings of rough lemon *(Citrus jambhiri* Lush.), Natsudaidai *(C. natsudaidai* Hayata), or Eureka lemon *(C. limon* (L.) Burm. f.), which were grown in 2.5-liter plastic pots in an insect-proof glasshouse. These rootstocks are susceptible to CTV infection. Grafting was judged successful when the scion survived more than 3 months after grafting. In the cases where the grafting was unsuccessful or when the growth of the grafted scion was poor, grafting was repeated. The growth of the grafted scion was graded good, poor, or very poor by comparing its growth to that of *Citrus* grafted on *Citrus*.

Inoculation with CTV. A severe strain of seedling yellows tristeza virus (CTV-SY) (17) was used. It was isolated originally from a tree of Kiyomi tangor, which is a hybrid of Miyagawa-Wase unshiu (*Citrus unshiu* var. *praecox* Tan.) × Trovita orange *(C. sinensis* Osbeck), planted at the Okitsu Branch, Fruit Tree Research Station. This strain caused severe stunting and yellowing in sour orange *(C. aurantium* L.) seedlings, and severe dwarfing and pittings in sour lime *(C. aurantifolia* (Christm.) Swing.) seedlings. Infected rough lemon seedlings were used as an inoculum source. Inoculation was achieved by grafting infected tissues to the rootstocks, except for Sydney hybrid, which was graft-inoculated to its stem directly. In some cases, inoculation to the rootstocks was done before graft of scion.

Inoculated plants were grown in the glasshouse, where the minimum temperatures were 20°C in winter and the maximum ranged from 25 to 35°C.

Assay for CTV infection. CTV infection was assayed by double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) using polyclonal antibodies against CTV. Young leaf midribs of the scions were tested by ELISA, except for *Microcitrus*, where young shoots were used because of its tiny leaves. Leaf midribs of shoots that sprouted from the rootstocks were also tested for CTV infection. These materials for ELISA were sampled 4 to 12 months after inoculation. Each 0.3-g sample was ground in 3 ml of extraction buffer consisting of phosphate-buffered saline containing 0.05% Tween 20 and 2% polyvinylpyrollidone. After centrifugation at 5,000 rpm for 10 min, the supernatant was used for ELISA. The midribs of CTV-free Etrog citron *(Citrus medica* var. *ethrog* Engl.) and CTV-infected Trovita orange were used as healthy and CTV-infected controls, respectively, in all tests.

Reactions were read spectrophotometrically at 405 nm (OD_{405}) using a Microplate Reader MTP-32 (Corona Electric Inc., Ibaraki, Japan). A positive reaction was defined as an OD_{405} three times that of the healthy control, according to the method of Irey et al. (8). The plants that tested positive were confirmed, and the plants that tested negative were tested again 1 to 2 years after inoculation.

RESULTS

Graft compatibility. The results of grafting are shown in Table 1. The rate of graft success ranged from 27 to 100%, and all the species used were graftable to *Cit-*

rus. Clausena anisata (Willd.) Hook. f. and *C. lansium* (Lour.) Skeeds, which are remote from *Citrus*, were grafted with 100% success, while *Microcitrus australis* and *Atalantia monophylla* DC., which are close to *Citrus*, were grafted with a low success rate.

The growth of grafted trees varied markedly among the species. The following eight species grew well on *Citrus* (similar to *Citrus* on *Citrus*): *Severinia buxifolia, Atalantia monophylla*, A. *citroides* Pierre ex Guill., *Clymenia polyandra* (Tan.) Swing., and *Fortunella polyandra* (Ridl.) Tan. in the subtribe *Citrinae* of the tribe *Citreae,* and *Swinglea glutinosa* (Blanco) Merr., *Feroniella lucida* (Scheff.) Swing., and *Feronia limonia* (L.) Swing. in the subtribe *Balsamocitrinae.* The species grafted on Natsudaidai, such as *Clymenia polyandra, Fortunella polyandra,* and *Swinglea glutinosa,* grew vigorously, even if inoculated with CTV-SY. Other species grew poorly or very poorly, and *Clausena anisata* grew so poorly that no samples could be collected for ELISA.

Susceptibility to CTV infection. The results of ELISA are shown in Table 2. All the shoots from the inoculated rootstocks were found infected with CTV, and their ELISA values were as high as those of the CTV-infected control. This confirmed the success of the original graft inoculation.

Fortunella polyandra, Clymenia polyandra, Microcitrus australis, and *Eremocitrus glauca* (Lindl.) Swing., which belong to the group of true citrus fruit trees of *Citrinae,* and Sydney hybrid were infected with CTV. Their ELISA values were higher than that of the CTV-infected control. This indicated that CTV multiplied abundantly in these plants.

Atalantia monophylla, *A. citroides,* and *Citropsis articulate* (Willd.) Swing., which belong to the group of near-citrus fruit trees of *Citrinae,* were also infected with CTV. The ELISA value was low in *A. citroides.*

Pleiospermium sp. and *Hesperethusa crenulata* (Roxb.) Roem., which belong to the group of primitive citrus fruit trees of *Citrinae,* were infected with CTV. The ELISA value for the former was high, while that of the latter was low. *Severinia buxifolia*-1 and *S. buxifolia* brachytic form were negative for CTV infection. But *S. buxifolia*-2 was positive and showed a relatively high value.

Triphasia trifolia (Burm. f.) P. Wils., which belongs to the subtribe *Triphasiinae* of *Citreae,* was not infected with CTV.

In the *Balsamocitrinae, Swinglea glutinosa* and *Aeglopsis chevalieri* Swing. were infected with CTV. On the other hand, *Aegle marmelos* (L.) Corr., *Feronia limonia,* and *Feroniella lucida* were not infected with CTV.

In the *Clauseneae,* the other tribe of *Aurantioideae, Clausena excavata* Burm. f. and *C. lansium*, which belong to the subtribe *Clauseninae,* were infected with CTV, but their ELISA values were relatively low. On the other hand, *Glycosmis pentaphylla* (Retz.) Correa, *Murraya koenigii* (L.) Spreng., and *M. paniculata* (L.) Jack were negative for CTV infection.

Merrillia caloxylon (Ridl.) Swing., which belongs to the *Merrilliinae,* another subtribe of *Clauseneae,* was infected with CTV, but the reaction by ELISA was low.

DISCUSSION

All the species used were graftable to *Citrus* rootstocks, although the rate of graft success varied. Zakaria et al. (22) reported that a high graft compatibility was obtained between closely related species of *Aurantioideae* plants. In this study, there was no clear relation between the rate of graft success and the classification order of *Aurantioideae.* And the growth of scions did not agree with the rate of graft success. In addition to graft compatibility, CTV inoculation may also have influenced the growth of some species. *Severinia buxifolia, Atalantia monophylla*, A. *citroides, Clymenia polyandra, Fortunella polyandra, Swinglea glutinosa,* and *Feronia limonia* grew well on *Citrus* rootstocks, confirming a previous report (2).

The study revealed that 15 species out of the 22 species tested could be infected with CTV. *Microcitrus australis, Swinglea glutinosa,* and *Aeglopsis chevalieri* were previously reported susceptible to CTV (4,5,10–12). *Citropsis gilletiana* Swing. & M. Kell. (belonging to the near-citrus fruit trees of *Citrinae*), *Pamburus missionis* (Wt.) Swing. (belonging to *Triphasiinae*), and *Afraegle paniculata* (Schum.) Engl. (belonging to *Balsamocitrinae*), not tested in this study, have also been reported susceptible to CTV (11,12). These observations suggest that CTV has a wide host range in plants of the *Aurantioideae.* The species that tested negatively for CTV by ELISA are probably immune to the strain of CTV used.

Clausena excavata, *C. lansium, Severinia buxifolia, Hesperethusa crenulata,*

Table 1. Genera evaluated for susceptibility to CTV, and source, rate of graft success onto *Citrus* rootstocks and growth of each

Genus, species	Type of material[a]	Source	Grafted rootstocks[b]	Graft success (%)[c]	Growth of grafted tree[d]
Tribe *Clauseneae*					
Subtribe *Clauseninae*					
Glycosmis pentaphylla	S	Saga Univ., Japan	10	40	Poor
Clausena excavata	S	Malaysia	5[e]	40	Poor
C. anisata	S	USA	5	100	Very poor
C. lansium	S	Taiwan	3	100	Poor
Murraya koenigii	S	Saga Univ., Japan	7	57	Poor
M. paniculata	B	USA	18	28	Very poor
Subtribe *Merrilliinae*					
Merrillia caloxylon	S	Malaysia	17	41	Very poor
Tribe *Citreae*					
Subtribe *Triphasiinae*					
Triphasia trifolia	S	Malaysia	6	67	Poor
Subtribe *Citrinae*					
Severinia buxifolia-1	U	USA	6	50	Good
S. buxifolia-2	B	Spain	5	100	Good
S. buxifolia Brachytic form	S	USA	8	50	Poor
Pleiospermium sp.	S	USA	6	83	Poor
Hesperethusa crenulata	B	Thailand	3	100	Poor
Citropsis articulata	S	USA	1	100	Poor
Atalantia monophylla	B	Thailand	11	27	Good
A. citroides	S	USA	5	100	Good
Eremocitrus glauca	S	Australia	14	71	Very poor
Microcitrus australis	B	USA	8	38	Poor
Sydney hybrid[f]	S	Australia	...	...	...
Clymenia polyandra	S	Papua New Guinea	5[g]	40	Good
Fortunella polyandra	S	Indonesia	3[g]	100	Good
Subtribe *Balsamocitrinae*					
Swinglea glutinosa	S	Indonesia	3[g]	67	Good
Aegle marmelos	S	Thailand	11	36	Poor
Aeglopsis chevalieri	S	USA	6	67	Very Poor
Feronia limonia	S	Malaysia	5	100	Good
Feroniella lucida	S	Thailand	10	40	Good

[a] S = seed; B = budwood; U = unknown.
[b] Rough lemon (*Citrus jambhiri*) was the primary rootstock.
[c] Grafting was judged successful when the scion survived more than 3 months.
[d] Good = growth comparable to *Citrus* on *Citrus*; very poor = shoot did not develop more than 5 cm during experiment; poor = intermediate.
[e] Eureka lemon (*C. limon*) was used as rootstock.
[f] A hybrid of *Microcitrus australis* × *M. australasica.*
[g] Natsudaidai (*C. natsudaidai*) was used as rootstock.

Atalantia monophylla, and *A. citroides* were infected with CTV in this study. These results are different from those reported by Knorr (11) and Müller and Garnsey (12). Possibly this is a reflection of differences in CTV strains used or in methods of inoculation and determination. Knorr (11) inoculated plants by aphids and determined infection only by observing specific symptoms. Müller and Garnsey (12) used a knife-slash method of inoculation and assayed for infection by ELISA.

Table 2. Results of enzyme-linked immunosorbent assay (ELISA) for CTV on *Citrus*-related genera graft-inoculated 4 to 27 months earlier

Genus, species	Plant no.	Date of grafting	Date of inoculation[a]	Results[b]
Glycosmis pentaphylla	1	3-11-92	3-11-92	–
	2	3-11-92	3-11-92	–
	3	3-11-92	3-11-92	–
Clausena excavata	1	8-29-90	8-29-90	+
	2	8-29-90	8-29-90	+
C. lansium	1	7-13-92	7-13-92	+
	2	7-13-92	7-13-92	+
	3	7-13-92	7-13-92	+
Murraya koenigii	1	3-11-92	3-11-92	–
	2	3-11-92	3-11-92	–
M. paniculata	1	7-1-92	7-13-92	–
Merrillia caloxylon	1	7-1-92	7-13-92	–
	2	7-1-92	7-13-92	+
	3	7-1-92	7-13-92	–
Triphasia trifolia	1	7-1-92	7-13-92	–
	2	3-6-93	5-23-93	–
	3	3-6-93	5-23-93	–
Severinia buxifolia-1	1	3-6-93	5-23-93	–
	2	3-6-93	5-23-93	–
	3	3-6-93	5-23-93	–
S. buxifolia-2	1	7-1-92	7-13-92	+
	2	7-1-92	7-13-92	+
	3	7-1-92	7-13-92	+
	4	7-1-92	7-13-92	+
	5	7-1-92	7-13-92	+
S. buxifolia Brachytic form	1	3-11-92	3-11-92	–
Pleiospermium sp.	1	7-1-92	7-13-92	+
	2	7-1-92	7-13-92	+
	3	7-1-92	7-13-92	+
Hesperethusa crenulata	1	7-1-92	7-13-92	+
	2	7-1-92	7-13-92	+
	3	7-1-92	7-13-92	+
Citropsis articulata	1	7-1-92	7-13-92	+
Atalantia monophylla	1	5-8-92	5-8-92	+
	2	5-8-92	5-8-92	+
	3	5-8-92	5-8-92	+
A. citroides	1	7-1-92	7-13-92	+
	2	7-1-92	7-13-92	+
	3	7-1-92	7-13-92	+
	4	7-1-92	7-13-92	+
Eremocitrus glauca	1	5-8-92	3-11-92	+
	2	5-8-92	5-8-92	+
Microcitrus australis	1	3-11-92	3-11-92	+
	2	3-11-92	3-11-92	+
	3	3-11-92	3-11-92	+
Sydney hybrid	1	...	3-6-93	+
Clymenia polyandra	1	10-6-89	9-26-88	+
Fortunella polyandra	1	10-6-89	9-26-88	+
	2	10-6-89	9-26-88	+
	3	10-6-89	9-26-88	+
Swinglea glutinosa	1	10-6-89	9-26-88	+
	2	10-6-89	9-26-88	+
Aegle marmelos	1	8-29-90	8-29-90	–
	2	3-17-92	3-17-92	–
	3	3-17-92	3-17-92	–
Aeglopsis chevalieri	1	7-1-92	7-13-92	+
Feronia limonia	1	3-6-93	5-23-93	–
	2	3-6-93	5-23-93	–
	3	3-6-93	5-23-93	–
Feroniella lucida	1	3-11-92	3-11-92	–
	2	3-11-92	3-11-92	–
	3	3-11-92	3-11-92	–

[a] Inoculation was performed by grafting infected tissues to rootstocks of *Citrus* spp., except for Sydney hybrid, which was graft-inoculated to its stem directly. In some cases, rootstocks were graft-inoculated before graft of scion.

[b] + = infected with CTV; – = not confirmed to be infected with CTV.

Müller and Garnsey (12) reported that *Aegle marmelos* was infected with CTV and developed vein clearing symptoms, whereas in this study this species was not infected even though its rootstock was CTV-positive. There are many reports that concentration of CTV varies depending on host plants, parts of tissue tested, and CTV strains (3,20). Therefore, the different results in *A. marmelos* may be due to the different CTV strains used. Knorr (11) reported that *Aeglopsis chevalieri* was infected with Argentine strains of CTV, but not with Florida strains.

Two sources of *Severinia buxifolia* from different countries showed different responses. This species probably contains subtypes that are either susceptible or immune to CTV, similar to those of *Poncirus trifoliata* (18,21). Further investigations on many individuals from different sources are needed.

The group of true citrus fruit trees of *Citrinae* contains *Citrus* and five other genera. Among them, *Eremocitrus*, *Clymenia,* and *Poncirus* are monotypic. In this study, *Eremocitrus glauca* and *Clymenia polyandra* were confirmed as hosts of CTV. It has been clarified that *Poncirus trifoliata* contains subtypes that are either susceptible or immune to CTV (18,21). All species of *Fortunella* are apparently hosts of CTV, since *F. margarita* (Lour.) Swing., *F. japonica* (Thunb.) Swing., *F. classifolia* Swing., and *F. obovata* Tan. were found susceptible to CTV (21); and *F. hindsii* (Champ.) Swing. (T. Yoshida, *unpublished*) and *F. polyandra* are also susceptible. There are no known CTV-immune species or cultivars in *Citrus.* Two species of *Microcitrus, M. australis* and *M. australasica*, have been previously reported susceptible to CTV (12,21).

As a result of these investigations, in the group of true citrus fruit trees, the trait of immunity to CTV has been found only in *Poncirus trifoliata.* Therefore, *P. trifoliata* is very important for CTV immunity breeding of citrus by the ordinary crossing method. This species probably obtained the trait of immunity after its speciation, because the trait has not been found in closely related genera.

This study revealed several species that tested negatively by DAS-ELISA and are probably immune. However, further studies on the mechanisms of immunity and its inheritance are necessary.

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